



Potential of forest thinning to mitigate drought stress: A meta-analysis



Julia A. Sohn^{*,1}, Somidh Saha¹, Jürgen Bauhus

Chair of Silviculture, University of Freiburg, D-79085 Freiburg, Germany

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ABSTRACT

Increasing frequency of extremely dry and hot summers in some regions emphasise the need for silvicultural approaches to increase the drought tolerance of existing forests in the short term, before long-term adaptation through species changes may be possible. The aim of this meta-analysis was to assess the potential of thinning for improving tree performance during and after drought. We used results from 23 experiments that employed different thinning intensities including an unthinned control and focused on the response variables: radial growth, carbon- and oxygen-isotopes in tree-rings and pre-dawn leaf-water potential. We found that thinning effects on the growth response to drought differed between broadleaves and conifers, although these findings are based on few studies only in broadleaved forests. Thinning helped to mitigate growth reductions during drought in broadleaves, most likely via increases of soil water availability. In contrast, in conifers, comparable drought-related growth reductions and increases of water-use efficiency were observed in all treatments but thinning improved the post-drought recovery and resilience of radial growth. Results of meta-regression analysis indicate that benefits of both moderate and heavy thinning for growth performance following drought (recovery and resilience) decrease with time since the last intervention. Further, growth resistance during drought became smaller with stand age while the rate of growth recovery following drought increased over time irrespective of treatment. Heavy but not moderate thinning helped to avoid an age-related decline in medium-term growth resilience to drought. For both closed and very open stands, growth performance during drought improved with increasing site aridity but for the same stands growth recovery and resilience following drought was reduced with increasing site aridity. This synthesis of experiments from a wide geographical range has demonstrated that thinning, in particular heavy thinning, is a suitable approach to improve the growth response of remaining trees to drought in both conifers and broadleaves but the underlying processes differ and need to be considered.

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1. Introduction

Forest ecosystems are particularly susceptible to extreme climatic events due to their relatively slow natural adaptation rates (Allen et al., 2010). More chronic water deficits due to increases in the frequency and intensity of extreme drought events have already led to decreases in forest productivity (Ciais et al., 2005; Phillips et al., 2009; Allen et al., 2015), increases of tree mortality and even widespread vegetation die-off in different regions of the world (van Mantgem et al., 2009; Allen et al., 2010; Adams et al., 2012). A higher resistance and resilience of forest ecosystems to extreme climatic events may be achieved through active adaptation strategies that aim to alter the composition of future forest stand; i.e., growing more drought-resistant

tree species and converting monocultures into mixed, uneven-aged forests (e.g., Lasch et al., 2002; Bolte and Degen, 2010; Brang et al., 2014). However, for existing forest stands that have not reached economic maturity, suitable short-term adaptation strategies need to be developed (Lindner, 2000; Lasch et al., 2002).

Over the last decades, increasing evidence shows that the maintenance of low stand densities can promote the vigour of individual trees and therefore thinning is suggested as an approach to climate adaptation in the short-term (Spittlehouse and Stewart, 2003; Anderson, 2008; Chmura et al., 2011). The positive impact of thinning on growth performance of trees during or after drought has been demonstrated for a number of genera and regions (Legoff and Ottorini, 1993; Cescatti and Piutti, 1998; Misson et al., 2003; McDowell et al., 2007; Kohler et al., 2010; Brooks and Mitchell, 2011; Giuggiola et al., 2013; Sohn et al., 2013). In addition, it has been shown that the higher resource acquisition capacity per tree with increasing growing space can reduce drought-induced

* Corresponding author.

E-mail address: julia.sohn@waldbau.uni-freiburg.de (J.A. Sohn).

¹ These authors contributed equally to this paper.

mortality (McDowell et al., 2008; Allen et al., 2010), fire risk and predisposition to insects and diseases (e.g., Chmura et al., 2011).

Residual trees become more vigorous after thinning inferior trees of a stand because resource availability increases along with growing space (Aussenac and Granier, 1988; Breda et al., 1995). Studies have revealed that forest stands with less dense canopies following thinning are often characterized by higher soil water availability for the residual trees (e.g., Aussenac and Granier, 1988; Misson et al., 2003; McDowell et al., 2003; Skov et al., 2004; Brooks and Mitchell, 2011). This is commonly attributed to reductions in stand transpiration and interception due to a lower leaf-area index (LAI) in thinned compared to unthinned stands (Breda et al., 1995). In addition, trees promoted through thinning may develop more extensive individual root systems over time, hence, increasing their capacity to extract water from the soil during and after drought periods compared to trees in unthinned stands (Whitehead et al., 1984; Aussenac and Granier, 1988; Misson et al., 2003).

However, thinning may also have negative effects on tree-water relations both in the short- and long-term. In recently thinned stands, higher wind speeds and greater penetration of solar radiation can lead to greater transpiration and evaporative water loss compared to unthinned stands (e.g., Lagergren et al., 2008; Brooks and Mitchell, 2011). Furthermore, the increase in leaf area of promoted trees and of ground vegetation after thinning can result in increases of stand-level transpiration and interception that may compensate or even reverse the previously described positive effects of thinning on water availability (e.g., Anders et al., 2006, for ground vegetation see references in Thomas et al., 1999). How fast and to what extent ground vegetation establishes in the years following thinning depends on a number of factors including thinning intensity and site quality (Nilsen and Strand, 2008).

Thinning intensity seems to be a major determinant of the magnitude and duration of the effects of thinning on growth. After less intense thinning, stand transpiration can return within few years to the pre-thinning level (Breda et al., 1995; Lagergren et al., 2008) while canopy closure proceeds more slowly and stand water use remains low for longer time periods after more intense thinning (Bren et al., 2010). How long stand-level LAI and thus water interception remain lower in thinned compared to unthinned stands should depend not only on how much LAI was reduced (thinning intensity) but also on the species' potential to occupy newly available growing space and on the intervals between thinning interventions (Sohn et al., 2016). Additionally, benefits of thinning for the growth response of trees during and after drought have been found to decrease with stand age due to higher water demands of larger trees in open compared to closed stands (D'Amato et al., 2013).

Drought impacts on tree physiology and growth are more detrimental in areas of limited water availability (Fritts et al., 1965; Hsiao et al., 1976; Ciaia et al., 2005; Bréda et al., 2006). Therefore, thinning effects on tree performance are likely more positive on sites where water is the main growth limiting factor.

This brief overview shows that tree growth and vitality may be influenced by thinning in quite different ways. The contrasting results among the studies reported above are likely related to dissimilar site conditions, tree species and thinning regimes. The aim of this paper is to systematically review the effects of thinning interventions on different variables of tree and stand performance during and after drought events through a meta-analysis. Based on results of existing studies, we hypothesize that thinning can help to improve the drought response of trees by mitigating tree performance during drought and by accelerating the recovery of tree performance after the drought. We specifically tested whether potential benefits of thinning for the tree response during and after drought events: (1) increase with thinning intensity, (2) decrease

with time elapsed since the first thinning intervention and with stand age, (3) differ between coniferous and broadleaved tree species, and (4) increase with site aridity.

2. Material and methods

2.1. Data compilation

Developing study selection criteria is a crucial first step in meta-analysis for the purpose of robust synthesis (Hungate et al., 2009). To be included in our meta-analysis, studies had to meet the following criteria: (1) they were carried out under field conditions in forests or plantations; (2) they permitted a comparison between at least two treatments, an un-thinned stand as control and at least one thinned stand; (3) a drought event had taken place during the study period (either the event was reported by the study itself or could be derived from data of local weather stations by us); (4) tree performance data were available for a period that spanned at least from one year before to one year after the drought; and (5) studies provided statistical information needed to perform a meta-analysis; i.e., mean, standard deviation of the mean and sample sizes of target variables. We searched the peer-reviewed literature using common databases like ISI Web of Knowledge, Google Scholar and CAB Abstracts for studies that quantified the potential of thinning to mitigate drought stress in trees. We used a factorial combination of search terms such as: "drought", "thinning", "thinning effect", "diameter growth", "height growth", "basal area increment", "leaf-water potential", "stomatal conductance", "sap-flow", and "isotopes". As of April 2016, we had found 158 articles using these keywords/queries. About 35 of these examined the effect of thinning on the drought response of trees but only 23 of these studies met our 5 selection criteria. The datasets included studies from 7 countries referring to temperate and Mediterranean regions and 2 datasets from the subtropics (Table 1, Fig. 1).

2.2. Target variables

We carefully selected target (response) variables that are considered to be suitable proxies for changes of tree vitality and that are sensitive to the combined effects of drought and competition intensity (thinning). Based on these considerations and the studies that fulfilled all selection criteria, 4 response variables were identified for our meta-analysis: (1) radial growth (provided as either tree-ring widths, or basal area increments or dendrometer measurements), (2) and (3) carbon and oxygen isotopic ratios in wood, as well as (4) pre-dawn leaf water potential (Table 1).

Tree ring series are commonly used to quantify tree and stand growth responses to climatic extremes at multiple spatial and temporal scales (Fritts, 1976). Additionally, annual radial growth is affected by neighborhood competition and thus is sensitive to thinning interventions (e.g., Fritts and Swetnam, 1989). Likewise, stable carbon and oxygen isotope ratios ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) in wood are good indicators of meteorological and environmental variations (Farquhar et al., 1989; Saurer et al., 1997; Schleser et al., 1999) and have been reported to be responsive to thinning as well (e.g., McDowell et al., 2006; Sohn et al., 2013). Pre-dawn leaf water potential is one of the most commonly used parameters for determining tree water status (see references in Turner, 1988). For example, elevated pre-dawn leaf potentials in recently thinned stands have been linked with higher relative extractable water in the soil due to lower crown interception and transpiration after canopy opening (e.g., Aussenac and Granier, 1988; Breda et al., 1995).

We extracted mean, standard deviation and number of sampled trees for all four target variables. As not all studies included analyses of all four target variables, the number of studies varied among target variables and thus among meta-analyses (Table 1).

Table 1

Site characteristics for thinning and drought studies included in the meta-analysis (Y = yes, MT = moderate thinning, HT = heavy thinning, C = unthinned control.).

Study	Author(s) of study	Target variables			Thinning variant	Country	Elevation (m asl)	Tree species	Stand age during drought	Stand age first thinning	Number of thinning inter-ventions	Time lag between last thinning and drought	Climatic region	Temperature (°C)	Rainfall (mm)		
		Radial growth	Water potential	$\Delta^{13}\text{C}$												$\delta^{18}\text{O}$	
1	Breda et al. (1995)		Y			MT, No	France	237	<i>Quercus petraea</i>	43	42	1	1	Temperate	9.2	744	
2	Brooks and Mitchell (2011)	Y		Y	Y	HT, No	Canada	350	<i>Pseudotsuga menziesii</i>	37	23	1	14	Temperate	8.9	1160	
3	Linares et al. (2009)	Y				MT, HT, No	Spain	1200	<i>Abies pinsapo</i>	60	59	1	1	Mediterranean	11	1200	
4	Corcuera et al. (2006)	Y				MT, No	Spain	900	<i>Quercus pyrenaica</i>	35	34	1	1	Mediterranean	9.5	794 & 449	
5	Dobner (2013)	Y				MT, HT, No	Brasil	950	<i>Pinus taeda</i>	25	5	MT = 5, HT = 4		Subtropical	16	1800	
6	Dobner et al. (2012)	Y				MT, HT, No	Brasil	900	<i>Eucalyptus dunnii</i>	6	2	2	4	Subtropical	16	1800	
7	D'Amato et al. (2013)	Y				MT, HT, No	USA	220	<i>Pinus resinosa</i>	76	45	4	7	Temperate	2.8	766	
8	Fernandes et al. (2016)	Y			Y	HT, No	Spain	943	<i>Pinus halepensis</i>	49	43	2	6	Mediterranean	14.1	477	
9	Giuggiola et al. (2016)	Y		Y		HT, No	Switzerland	620	<i>Pinus sylvestris</i>	83	40	1	43	Temperate	10.1	672	
10	Guillemot et al. (2015)	Y				MT, HT, No	France	1170	<i>Cedrus atlantica</i>	38	25	2	13	Mediterranean	9.6	1076	
11	Martin-Benito et al. (2010)	Y				MT, HT, No	Spain	1050	<i>Pinus nigra</i>	42	32	1	10	Temperate	11.3	663	
12	McDowell et al. (2003)	Y		Y		HT, No	USA	1000	<i>Pinus ponderosa</i>	244	237	1	7	Temperate	6	1667	
13	McDowell et al. (2006)	Y		Y	Y	MT, HT, No	USA	2200	<i>Pinus ponderosa</i>	70	43	3	5	Dry temperate	6	564	
14	Moreno and Cubera (2008)		Y			HT, No	Spain	380	<i>Quercus ilex</i>	na	na	na	na	Mediterranean	16.2 & 14.7	506 & 816	
15	Pérez-de-Lis et al. (2011)	Y				MT, HT, No	Spain	1650	<i>Pinus canariensis</i>	42	23	1	19	Mediterranean	15.9	476	
	Pérez-de-Lis et al. (2011)	Y				MT, HT, No	Spain	1700	<i>Pinus canariensis</i>	38	26	1	12	Mediterranean	15.9	476	
16	Primicia et al. (2013)	Y				MT, No	Spain	642	<i>Pinus sylvestris</i>	36	30	1	6	Mediterranean	12	913	
17	Rodríguez-Calcerrada et al. (2011)	Y	Y			MT, No	France	270	<i>Quercus ilex</i>	54	51	1	3	Mediterranean	13.1	914	
	Rodríguez-Calcerrada et al. (2011) (through fall reduction)	Y	Y			MT, No	France	270	<i>Quercus ilex</i>	54	51	1	3	Mediterranean	13.1	914	
18	Simonin et al. (2006)		Y			HT, No	USA	2080	<i>Pinus ponderosa</i>	70	69	1	1	Temperate (dry)	6.7	542	
19	Sohn et al. (2013) (Freising)	Y		Y	Y	MT, HT, No	Germany	500	<i>Picea abies</i>	56	27	4	7	Temperate	7.9	790	
	Sohn et al. (2013) (Göggingen site)	Y		Y	Y	MT, HT, No	Germany	650	<i>Picea abies</i>	56	27	5	6	Temperate	7.5	780	
20	Stoneman et al. (1996)		Y			MT, HT, No	Australia	267	<i>Eucalyptus marginata</i>	65	40	1	15	Mediterranean	16	1100	
21	van der Maaten (2013)	Y				MT, HT, No	Germany	750	<i>Fagus sylvatica</i>	96	100	1	4	Temperate	7	900	
22	Sohn et al. (2016) (Fuhrberg site)	Y		Y	Y	MT, HT, No	Germany	40	<i>Pinus sylvestris</i>	22	6	MT = 2, HT = 3		Temperate	9.9	683	
	Sohn et al. (2016) (Weiden site)	Y		Y	Y	MT, HT, No	Germany	400	<i>Pinus sylvestris</i>	54	27	MT = 4, HT = 3		MT = 2, HT = 13	Temperate	7.8	696
	Sohn et al. (2016) (Burglen-genfled site)	Y		Y	Y	HT, No	Germany	355	<i>Pinus sylvestris</i>	41	16	2	13	Temperate	8.5	536	
	Sohn et al. (2016) (Schwetzingen site)	Y		Y	Y	MT, HT, No	Germany	115	<i>Pinus sylvestris</i>	21	8	MT = 3, HT = 2		MT = 2, HT = 6	Temperate	10.9	659
23	Thomas and Waring (2015)	Y				HT, No	USA	2350–2530	<i>Pinus ponderosa</i>	83	40	1	1	Temperate	4.7	432	

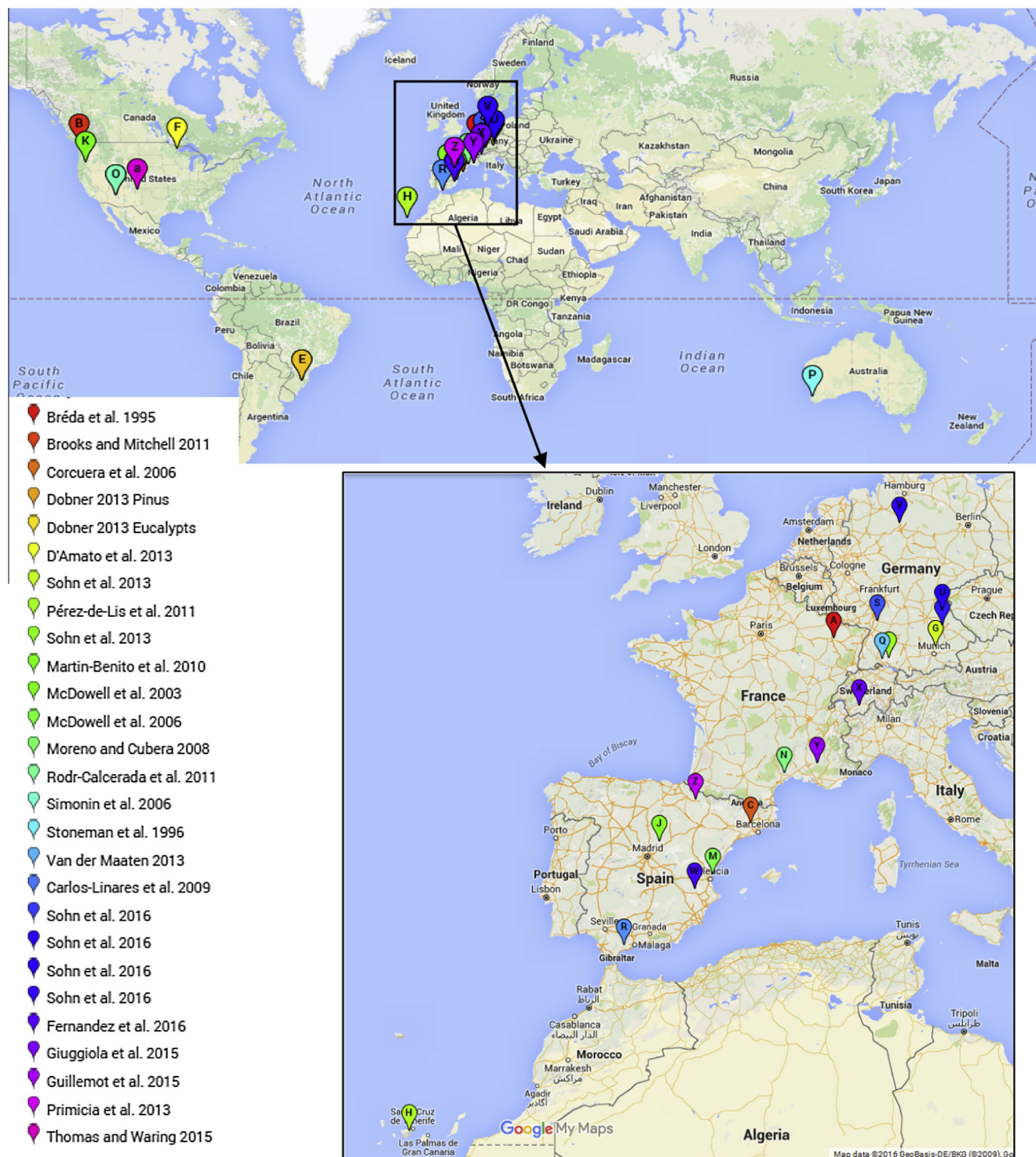


Fig. 1. Geographical location of the 23 published papers and original datasets that met all selection criteria and were used in our meta-analysis. <https://www.google.de/maps/d/u/0/edit?mid=1f00YC9d1fjezBj1xktRU7ViUB0g>.

As we aimed to quantify the influence of thinning intensity on the target variables (Hypothesis 1), we classified thinning treatments applied in the different studies into 2 intensities that were based on the magnitude of stand basal area (BA) reductions (in % compared to pre-thinning levels): a “moderate thinning” treatment for BA reductions of less than 40% and a “heavy thinning” treatment for BA reductions of more than 40%.

For each dataset, we used stand age at the time of drought and calculated the number of years that had elapsed between the drought event and the most recent thinning intervention (from

here on referred to as the “thinning lag”) for testing hypothesis 2. We used “thinning intensity” (i.e. moderate vs. heavy thinning) and “taxonomic class” (conifers vs. broadleaves) as categorical explanatory variables or “moderators” for testing Hypothesis 1 and 3, respectively. Further, for testing Hypotheses 4, we used a simplified site aridity index (i.e., HKL-index, see Döring et al., 2011) for each site as,

$$HKL = \frac{3 * T_{mean}}{Precip}$$

where T_{mean} is the mean annual temperature, and $Precip$ is the sum of annual rainfall. These were the only climatic variables that could be extracted commonly from all studies used in the meta-analysis. Despite its simple calculation, the HKL-index has been proven to be highly correlated with other aridity indices (Döring et al., 2011).

The categorical moderator “thinning intensity” was used for analyzing the effect of thinning on all four target variables. However, the categorical moderator “taxonomic class” (Hypothesis 3) and the continuous moderators “thinning lag”, “stand age” (Hypothesis 2) as well as “site aridity” (hypothesis 4) could be used only as a moderators when analyzing the effect of thinning on the response variable “radial growth” due to the low number of studies for the other 3 target variables.

2.3. Meta-analysis

2.3.1. Effect sizes

Logical selection of the effect size metrics based on sound biological models is a prerequisite for meaningful and robust meta-analyses (Osenberg et al., 1997). On the one hand, the magnitude of differences in tree performance throughout drought episodes among thinned and unthinned stands is likely to vary depending on the level of thinning intensities applied. On the other hand, when determining the potential of thinning to improve the drought response of trees, one has to separate between thinning effects originating either from the mitigation of stress during a drought event itself or from an accelerated recovery of tree performance following drought stress (Kohler et al., 2010; Lloret et al., 2011). Based on this concept, we calculated 2 types of effect sizes:

First, response ratios that compare the treatment effect for each of the four target variables were calculated as relative differences between thinned and unthinned stands as:

$$E_i = \frac{X_{Ti}}{X_{UTi}}$$

where E_i is the response ratio for a variable (e.g., annual basal area growth) of the study i , and X_{UTi} and X_{Ti} are the means of the same variable (e.g., annual mean of basal area growth) for study i in thinned (T) and unthinned (UT) stands, respectively. These response ratios were calculated separately for each year of a period comprising pre-drought year(s), drought year, and post-drought year(s); in the following we refer to these periods as “drought periods”. By doing this, we obtained response ratios that compare the growth performance of trees growing in thinned stands (moderately vs. heavily) with that of trees from unthinned control stands for each year of a drought period. As effect sizes are ratios, a value of 1 denotes no difference between thinned and unthinned stands while values below or above 1 suggest that the magnitude of effects in the thinned stands was smaller or larger than in the unthinned stands (Osenberg et al., 1997).

Secondly, in order to determine if thinning can help to improve the tree response during and after drought events, we calculated effect sizes for the response variable radial growth as indices of resistance (RES), recovery (REC) and resilience (RESIL) separately for each treatment based on the concept proposed by Lloret et al. (2011) as:

$$RES = \frac{X_{DY}}{X_{PreDY(s)}}$$

$$REC = \frac{X_{PostDY(s)}}{DY}$$

$$RESIL = \frac{X_{PostDY(s)}}{X_{PreDY(s)}}$$

where X_{DY} is the radial growth during the drought year, $X_{PreDY(s)}$ is the (mean) basal area growth during the pre-drought year(s) and $X_{PostDY(s)}$ is the (mean) basal area growth during the post-drought year(s). For each of the three Lloret-indices, we calculated 2 types of values that differed in terms of the number of years for the pre- and post- drought period; a short-term index using the value referring to 1 year before or after the drought and a medium-term index using the mean of the 3 years before or after the drought event (see Kohler et al., 2010; Lloret et al., 2011).

2.3.2. Weighting functions

We followed the mixed-model approach for conducting the meta-analysis with categorical explanatory variables. This combines a random and mixed effect approach for the calculation of weights based on variances between and within categories; the latter tests if categories (e.g. moderately thinned stands) are also internally heterogeneous (Gurevitch and Hedges, 1999). Thus, we calculated weights using variances from both fixed and random effects models, and then, based on the derived weights, performed categorical random effect meta-analysis, which is also known as mixed-effect models in meta-analysis and analogous to mixed-effect models in ANOVA (Gurevitch and Hedges, 1993; Hedges and Vevea, 1996).

2.3.3. Relationships between effect sizes and categorical variables

Meta-analysis using the mixed-model approach was performed in 3 major steps (see Saha et al., 2012 for detailed statistical descriptions): First, a fixed effects meta-analysis was conducted to determine the values of the summary statistics i.e., effect size, variance and total heterogeneity. Secondly, we calculated an estimate of the pooled trial variance (or between trial variance), necessary to generate the weights for the random effects models, by using summary statistics. Finally, the derived weights were used in a mixed-effects model to calculate the global cumulative effect as well as the associated confidence intervals. In addition, in the mixed-effect model, total heterogeneity was further divided into (a) heterogeneity explained by the categories and (b) the residual error heterogeneity.

2.3.4. Relationships between effect sizes and continuous variables

We investigated the relationships between effect sizes and the 3 continuous explanatory variables: thinning lag, stand age and site aridity through a meta-regression as suggested by Rosenberg et al. (2000) as,

$$E_i = b_0 + b_1 X_i + \varepsilon$$

where E_i and X_i are the effect size and continuous explanatory variable, respectively, for the i th study; and b_0 and b_1 are the intercept and slope (i.e. coefficient) of the meta-regression, respectively. The coefficient and slope were weighted by within and between-study variance and standard errors were calculated for both. Dividing the slope and intercept by the corresponding standard error yields their Z-score, which is then compared to a normal distribution in order to determine whether they are statistically significant. A significant regression coefficient (i.e., slope) implies that the independent variable explains a significant portion of the variation in effect sizes.

2.3.5. Statistical analyses

For the categorical meta-analysis, logarithmic transformations of response ratios for individual studies were performed and corresponding variances were calculated. For the pooled cumulative estimates of response ratios, the logarithmic transformation was reversed for easier interpretation (Agardh et al., 2011). Because the number of studies in our meta-analysis was rather low from some comparisons, we calculated 95% bootstrap confidence

intervals of both effect sizes (response ratios, Lloret's indices) and model coefficients based on 999 iterations (Adams et al., 1997; Verschuyt et al., 2011; Saha et al., 2012). We considered a combined effect to be significant, if the lower or upper limit of the derived confidence interval did not overlap the horizontal line at 1, implying a significant difference in thinned and unthinned stands for the analyzed response variable. All statistical analyses were done using MetaWin 2.0 and R 2.14.0 (Rosenberg et al., 2000; R Development Core Team, 2011).

2.4. Normalization of wood isotopic data to derive drought-anomalies

We interpreted drought-related differences in tree-ring $\Delta^{13}\text{C}$ and $\delta^{18}\text{O}$ among differently thinned stands according to theoretical predictions for changes of stomatal conductance (g_s) and photosynthetic capacity (A_{\max}) based on the conceptual framework proposed by Scheidegger et al. (2000). In order to deduce the physiological response of trees to drought, we used a normalization approach that reduces sources of variance, similar to the approach used by Barnard et al. (2012). In order to make our isotope analysis comparable to that of Barnard et al. (2012), we used $\delta^{13}\text{C}$ rather than $\Delta^{13}\text{C}$ for calculating drought-anomalies. For each thinning treatment and study, we first averaged values of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ referring to the years before and after the drought-event in order to obtain the non-drought mean (similar to the normalization using the temporal mean in Fig. 5 of Barnard et al., 2012). Next, we calculated the difference between the drought-year value and the non-drought mean for both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ to obtain drought-year anomalies of both isotopes from the non-drought baseline. Finally, we plotted normalized values of $\delta^{13}\text{C}$ against those of $\delta^{18}\text{O}$ of all studies separately for each thinning treatment so that deviations from zero represent variation of isotope values in the drought-year compared to the non-drought mean.

3. Results

3.1. Effects of thinning-regime, stand age and site aridity on radial growth

3.1.1. Effect of thinning intensity on radial growth during drought periods

This section is based on the summary statistics for the effect sizes that were calculated as response ratios for comparing radial growth of trees in thinned and unthinned stands separately for each year of the drought period. Radial growth was significantly

higher in moderately and heavily thinned stands when compared to unthinned stands throughout the entire drought period; i.e., effect sizes were always significantly larger than 1 (Fig. 2). Compared to unthinned stands, radial growth was on average 125% higher in heavily thinned stands and 47% higher in moderately thinned stands. The growth difference between thinned and unthinned stands fluctuated by a similar magnitude of ca. 30% among years in the 2 thinning treatments (Fig. 2). Trees in heavily thinned stands grew significantly faster than trees in moderately thinned stands in all years except for the drought-year itself, during which confidence intervals overlapped (Fig. 2).

3.1.2. Effect of thinning intensity on the response of radial growth during and after drought

The magnitude of short- and medium-term resistance, recovery and resilience of radial growth was not significantly different between thinned and unthinned stands; i.e. confidence intervals of effect sizes calculated as Lloret-indices overlapped among the 3 treatments (Fig. 3). Growth during the drought-year was significantly reduced compared to the pre-drought year(s) in all treatments, i.e. short- and medium-term resistance was always significantly smaller than 1 (Fig. 3a). Short- and medium-term recovery of radial growth was significantly larger than 1 in all 3 treatments; i.e., thinned and unthinned stands had significantly faster growth rates (by 26–30% and by 42–67%, respectively) in the post-drought year(s) when compared to the drought year (Fig. 3b). Despite larger values of short- and medium-term recovery in unthinned compared to thinned stands, no significant difference among treatments was found due to the large confidence intervals in unthinned stands (Fig. 3b). Effect sizes of both short and medium-term resilience of radial growth were close to 1 in all treatments (0.88–0.96) indicating similar growth rates in the post-drought year(s) compared to pre-drought year(s) irrespective of treatment (Fig. 3c).

3.1.3. The influence of thinning lag and stand age on drought responses of radial growth

We found a significant negative relationship ($p < 0.001$) between the number of years since the last thinning intervention; i.e. the thinning lag, and short-term and medium-term growth recovery as well as resilience to drought for both thinning treatments (see appendix).

In contrast, the effect of thinning lag on the resistance of radial growth during drought was (although significant in all cases) not consistent for the two thinning treatments (see appendix): For

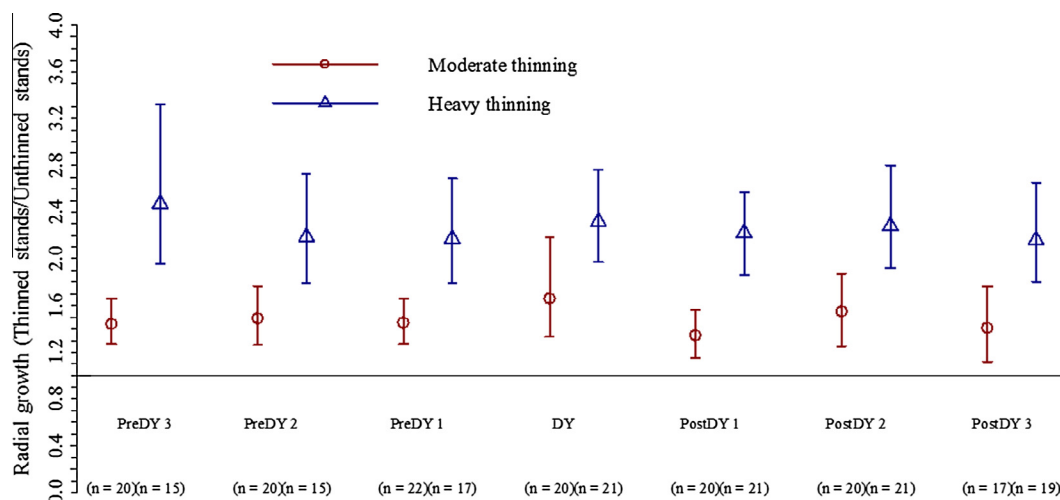


Fig. 2. Global cumulative effect sizes as well as associated confidence intervals for the response ratios that compare annual radial growth of trees in (moderately or heavily) thinned vs. unthinned stands. DY = drought-year, PreDY = pre-drought year and PostDY = post-drought year. Sample size (n) was 15–21.

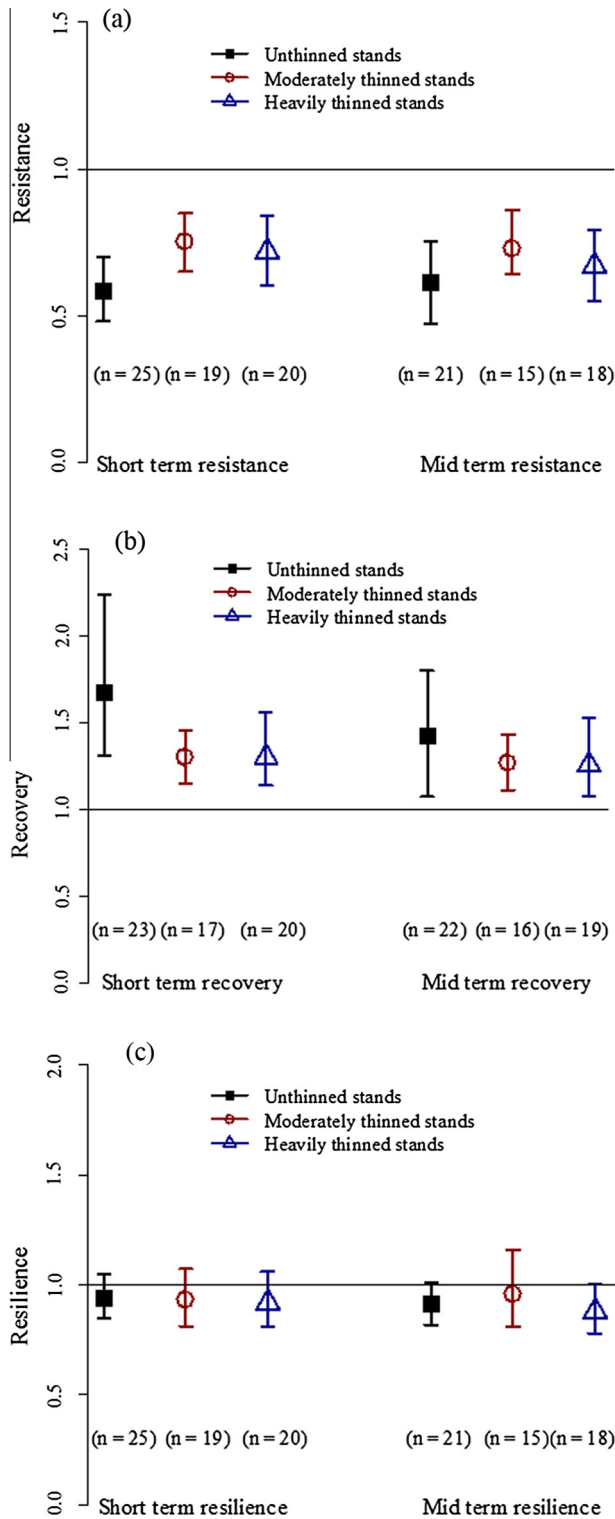


Fig. 3. (a–c) Global cumulative effect sizes as well as associated confidence intervals for the resistance (a), recovery (b), and resilience (c) in relation to drought among differently thinned stands. For each of the 3 *Lloret*-indices, we calculated (left) a short-term index using the value referring to 1 year before (for resistance and resilience) or after the drought (recovery and resilience) and (right) a medium-term index using the mean of the 3 years before or after the drought event (see *Lloret et al., 2011; Kohler et al., 2010*). Values of 1 mean for resistance that no growth reduction has taken place, at 0.5 a 50% reduction occurred. For recovery, a value of 1 means that growth after drought stayed at the level of the drought year. For resilience, a value of 1 indicates that growth after the drought returned to the pre-drought level. Sample size was $n = 15$ – 25 .

the moderate thinning treatment, we found a positive effect of the thinning lag on short-term resistance and a negative effect of the thinning lag on medium-term resistance while the opposite was observed for the heavy thinning treatment.

The resistance of radial growth during drought decreased with stand age in all treatments except for medium-term resistance in moderately thinned stands, which was not affected by stand age (see appendix). In contrast, stand age had a positive effect on growth recovery following drought in all treatments except for short term recovery in moderately thinned stands, where no relationship was found (S1). In contrast, resilience did not change with stand-age with the exception of a positive effect of stand age on medium-term resilience in heavily thinned stands (see appendix).

3.1.4. Effects of thinning on the drought response of radial growth in broadleaves vs. conifers

The response of radial growth during (resistance) and following drought (recovery and resilience) differed markedly between conifers and broadleaves. In coniferous stands, short-term resistance of radial growth during drought was similar among treatments with growth reductions during the drought year amounting to values between 31 and 39% when compared to pre-DY levels (Fig. 4a). In contrast, short-term resistance of radial growth was higher in broadleaved trees from thinned than from unthinned stands. The latter suffered average growth reductions of 55% during the drought year (Fig. 4a). For conifers, the short-term recovery of radial growth following drought was higher in thinned than in unthinned stands, which had a recovery smaller than 1 (Fig. 4b). In broadleaved stands, the recovery of radial growth in the post-DY in the control stands was highly variable and not significant. This was the only treatment with growth reductions during the drought year (Fig. 4b).

In coniferous stands, growth in the post-DY was reduced by a similar magnitude of 10–13% compared to pre-DY growth-levels in all treatments, but this incomplete short-term resilience was significantly lower than 1 only in the unthinned stands (Fig. 4c). In broadleaved stands, short-term resilience increased with thinning intensity and was significantly larger than 1 in thinned stands (Fig. 4c).

3.1.5. Relationship between drought responses of radial growth with site aridity

Results from our meta-regression analysis indicated that the relationship between site aridity and the growth response during and after drought events was similar in unthinned and heavily thinned stands but distinctly different in moderately thinned stands. Both short- and medium-term resistance of radial growth during drought increased with site aridity in unthinned stands and the same was found for medium-term resistance in heavily thinned stands (see appendix). In contrast, for moderately thinned stands, short-term resistance was not influenced by site aridity and medium-term resistance even decreased with site aridity (see appendix). In unthinned and heavily thinned stands, short-term and medium-term recovery of growth following drought decreased with site aridity and the same was found for short-term and medium-term resilience in heavily thinned stands. The opposite was found for moderately thinned stands, where short-term and medium-term recovery and resilience increased with site aridity.

3.2. Effect of thinning intensity on isotopic composition of tree rings before, during and after drought

Results in this paragraph refer to the summary statistics of effect sizes that were calculated as response ratios of $\Delta^{13}\text{C}$ and $\delta^{18}\text{O}$ comparing thinned and unthinned stands separately for each year of the drought period. Moderately thinned stands were simi-

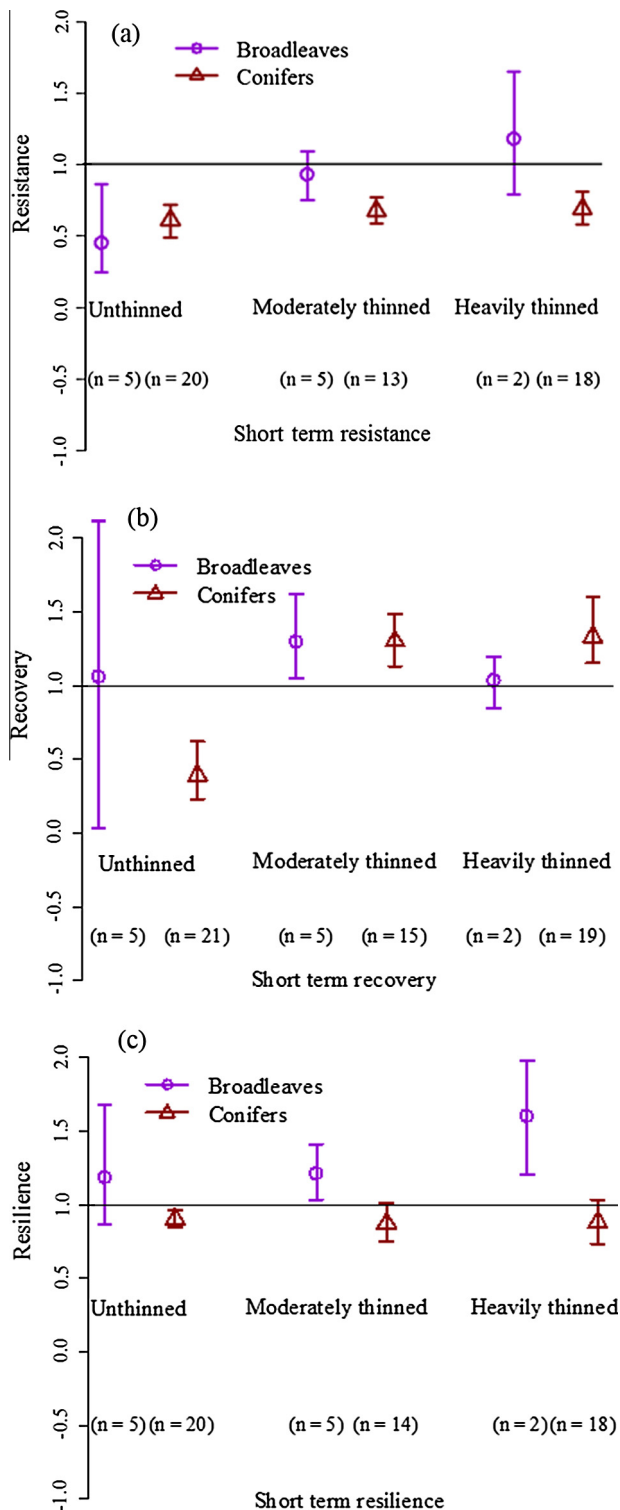


Fig. 4. (a–c) Global cumulative effect sizes as well as associated confidence intervals for the 3 drought response variables (resistance: a, recovery: b, and resilience: c) among differently thinned stands separately for coniferous and broadleaved stands. Each of the 3 *Lloret-indices* was calculated using the value referring to the drought year and the value for 1 year before (for resistance and resilience) or after the drought (recovery and resilience) (see [Lloret et al., 2011](#); [Kohler et al., 2010](#)). Sample size was $n = 2$ –20.

lar in $\Delta^{13}\text{C}$ compared to unthinned control stands throughout the drought period except for 1 significantly larger value in the second year before the drought (Fig. 5a). Heavily thinned stands were significantly lower in $\Delta^{13}\text{C}$ compared to the control during most

years of the drought period. Thinned stands were similar in $\delta^{18}\text{O}$ compared to unthinned stands in the 2 years preceding the drought and during the drought year in moderately thinned stands (Fig. 5b). In contrast, $\delta^{18}\text{O}$ was significantly higher in thinned than in unthinned stands in the post-drought period, and during the drought year it was higher in heavily thinned stands when compared to controls (Fig. 5b).

When normalizing the drought-year values by the non-drought mean to calculate drought anomalies for both wood isotopes, all treatments displayed higher $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in the drought-year (almost all values are in the upper right quadrant of Fig. 6a–c). This indicates a reduction in stomatal conductance at constant photosynthesis and therefore increased water-use efficiency during the drought-year in the majority of studies. In addition, normalized $\delta^{13}\text{C}$ tended to increase with normalized $\delta^{18}\text{O}$ in heavily stands ($p < 0.1$; Fig. 6c). In the case of moderately thinned and unthinned stands, the range of variation was more equally distributed for normalized values of both isotopes although the range of $\delta^{13}\text{C}$ was 1 and 0.8‰ greater than the range of $\delta^{18}\text{O}$, respectively (Fig. 6a, b).

3.3. Effect of thinning intensity on leaf-water potential during drought

Only few studies reported pre-dawn leaf water potential in thinning experiments. Response ratios (thinned vs. unthinned stands) of pre-dawn leaf water potential in the drought year were significantly smaller than 1 in both moderately and heavily thinned stands when compared to the unthinned control (Fig. 7). This indicates less negative water potentials (measured in negative units) in thinned compared to unthinned stands. Compared to unthinned stands, response ratios were 26% and 54% lower in moderately and heavily thinned stands, respectively, indicating highest soil water availability in the latter stands (Fig. 7).

4. Discussion

This meta-analysis showed that thinning of forest stands has the potential to improve physiological and growth performance of trees during and after drought events. However the response of trees to drought varied with thinning intensities, taxonomic class (conifer vs. broadleaved), time since the last thinning and stand age, and site aridity.

4.1. Thinning-related improvements of radial growth throughout the drought period increase with thinning intensity

Both moderate and heavy thinning allowed trees to maintain significantly higher growth levels before, during and after drought events when compared to trees in unthinned stands. In agreement with our first hypothesis, benefits increased with thinning intensity: after heavy thinning, growth levels were raised 3 times more above control values at a similar inter-annual variability when compared to the moderate thinning.

Despite these thinning-related benefits to radial growth in all years of the drought period, deviations of C- and O-isotope ratios in wood during the drought year from the non-drought baseline (Fig. 6) indicate a decrease in stomatal conductance at constant photosynthesis during the drought year in all treatments (as indicated by the Scheidegger model, see inserted arrows in Fig. 6). Thus, higher tree growth rates in all years including the drought year in thinned compared to unthinned stands were decoupled from the drought-signal of C and O isotopes in tree rings. This phenomenon, which had also been described by [Sohn et al. \(2013\)](#) for differently thinned stands of Norway spruce, is likely the result of remobilisation of non-structural carbon that was fixed in previous year(s) for wood formation ([Kagawa et al., 2006](#); [Richardson et al., 2013](#); [Gessler et al., 2014](#)). It would therefore be interesting to see,

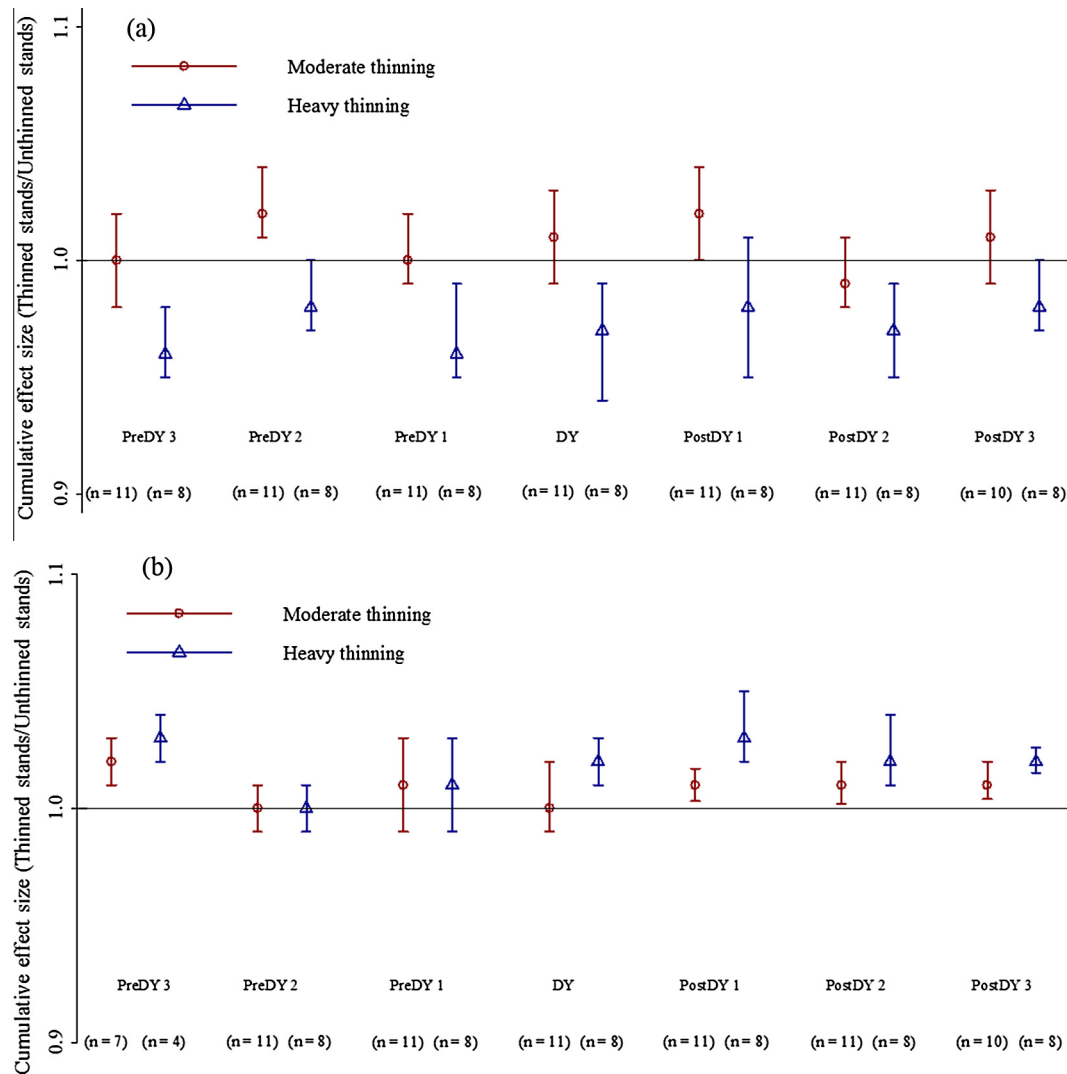


Fig. 5. (a and b) Global cumulative effect sizes as well as associated confidence intervals for the response ratios that compare (a) carbon discrimination and (b) oxygen isotopic composition of tree rings in (moderately or heavily) thinned vs. unthinned stands. DY = drought-year, PreDY = pre-drought year and PostDY = post-drought year. Sample size was $n = 4$ –11.

whether thinning may still improve radial growth in droughts that last for several years. However, our data set contained only seasonal droughts confined to 1 year.

In addition, the diverging results for growth and O-isotopes during and after drought may be also the result of short-comings of the dual isotope approach as it assumes that source water does not change between treatments and that all $\delta^{18}\text{O}$ changes are indeed related to stomatal conductance (Roden and Siegwolf, 2012). This assumption may not necessarily apply when comparing isotope data from thinned and unthinned stands as source-water usage is likely to differ among trees that differ in terms of growing space (Kerhoulas et al., 2013; Sohn et al., 2014). In addition, in thinning experiments in *Pinus ponderosa* stands, where gas exchange was measured directly for leaves in cuvettes, it has been shown that thinning often increases net photosynthetic rate and stomatal conductance also during dry periods (Feeney et al., 1998; Kolb et al., 1998; Stone et al., 1999; Skov et al., 2004).

In addition, results for isotopes in this meta-analysis refer to coniferous stands only. Hence it remains to be tested, how the drought signal of isotopes in wood matches that of radial growth in broadleaved stands.

Although growth differences between thinned and unthinned stands were largest during the drought year, there was no signifi-

cant effect of thinning intensity on the growth response during or after drought when analyzing all studies jointly (Fig. 3). In the following, we will elucidate how differences between the two taxonomic classes (conifers vs. broadleaves) may have masked such a global effect of thinning intensity.

4.2. Thinning mitigates growth reductions during drought in broadleaves and improves growth performance following drought in conifers

In accordance with our third hypothesis, the effects of thinning on the growth response to drought differed between broadleaves and conifers: In the former, thinning mitigated radial growth reductions during drought (resistance), whereas it appeared that thinning improved growth following drought (recovery and resilience) in the latter. However, owing to the low number of studies in broadleaved forests and the resulting imbalance between these studies and those in coniferous forests, the differences identified here need to be viewed with caution. They may be regarded as hypotheses that should be tested further, ideally with experiments that compare thinning effects between different species on the same site.

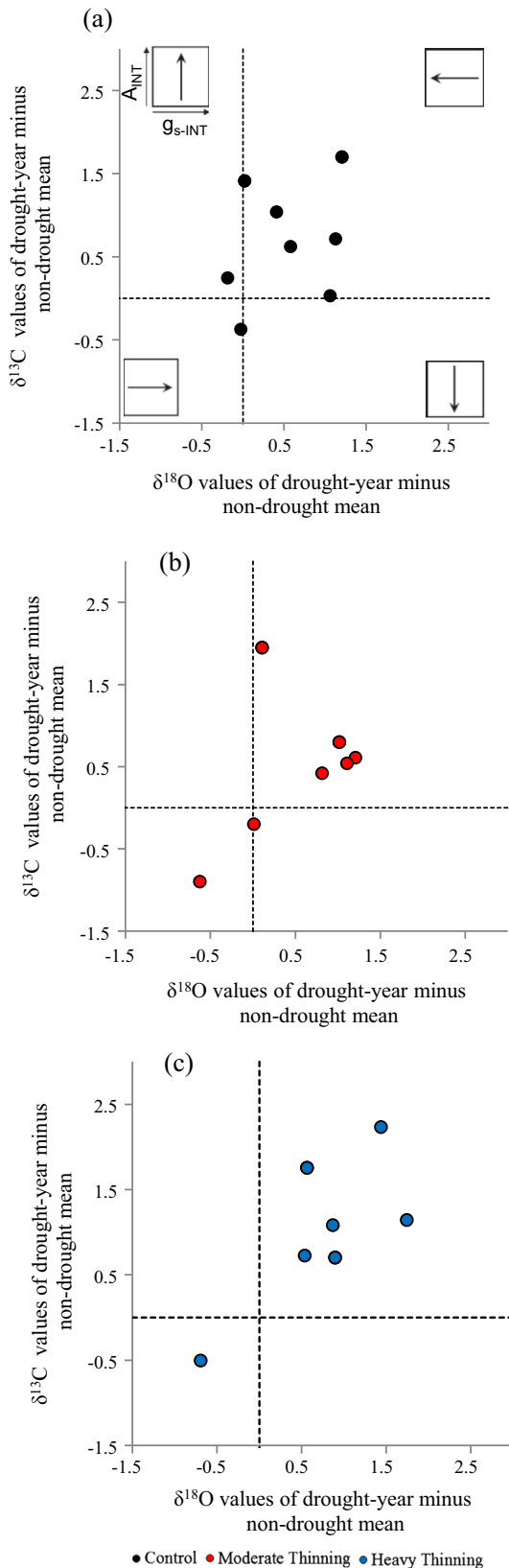


Fig. 6. (a–c) Drought anomalies of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ (values of drought-year minus non-drought mean) for unthinned control (a), moderately thinned (b) and heavily thinned stands (c). Points in each quadrant reflect the drought-related response combination of photosynthesis and stomatal conductance ($A_{\text{INT}}-g_{\text{sINT}}$) as indicated by the arrows in (a) based on the Scheidegger et al. (2000) model.

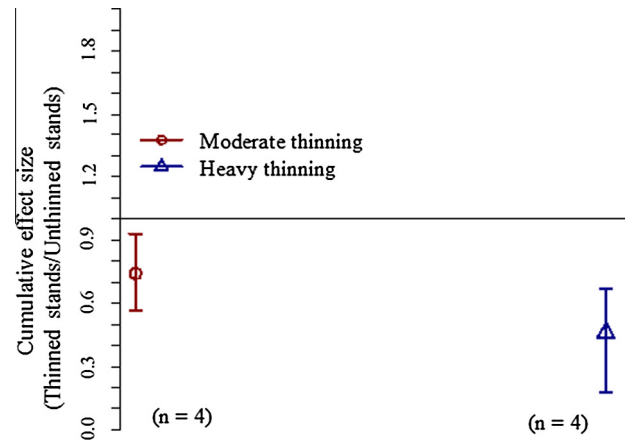


Fig. 7. Global cumulative effect sizes as well as associated confidence intervals for the response ratios that compare pre-dawn leaf water potential of trees in (moderately or heavily) thinned vs. unthinned stands; DY = drought-year, Pre-DY = pre-drought year and PostDY = post-drought year. Sample size was $n = 4$.

In broadleaves, the short-term resistance of radial growth during drought increased with thinning intensity, thus corroborating Hypothesis 1. These benefits of thinning are supported by the results for pre-dawn leaf water potential - which stem mostly from studies in broadleaves. Here, leaf water potentials during drought were increasingly less negative with thinning intensity, indicating increasing soil water availability with reductions in stand density. However, most studies reporting the target variable leaf-water water potential originated from *Quercus* stands from drier regions (studies 1, 14, 17 and 20), where tree species typically develop very deep root systems (Canadell et al., 1996; Schenk and Jackson, 2005). In addition, most of the tree ring width in this ring-porous genus is produced in spring, before severe water shortages in drought years occur (Zweifel et al., 2006; Foster et al., 2015). Therefore, it remains unclear if the observed pattern applies more widely to thinned stands of broadleaves.

In conifers, significant growth reductions of 30–40% during drought were found in all stands irrespective of thinning treatment. This is in agreement with the drought-anomalies of both isotopes, which indicated a reduction in stomatal conductance during drought years in the majority of studies irrespective of thinning treatments. Thus, in conifers, for a wide range of stand densities, significant growth reductions during drought occur despite increases in water-use efficiency.

Conifer trees in thinned stands reached pre-drought growth levels within 1 year after the drought. The finding that thinning improved growth performance following drought but not growth resistance during drought in conifers is in line with results for Norway spruce (Sohn et al., 2013). Since the first thinning intervention had been conducted several years ago in most conifer stands of this meta-analysis (except for studies 3 and 18), trees in thinned stands should have developed more foliage and fine-root biomass compared to trees in unthinned stands by the time of the drought event. Hence, larger above- and below-ground surfaces of may have allowed these trees to take more quickly advantage of improving conditions resulting in faster and more complete recovery of radial growth following drought as compared to trees in unthinned control stands. In contrast, during drought events, when soil water stores are entirely depleted, the larger crown surface areas of trees in thinned stands may have increased transpirational demand resulting in no benefits of thinning for mitigating growth reductions.

The greater benefits of thinning for growth resistance during drought in broadleaves when compared to conifers may be caused

by composition of this taxonomic group which comprised mainly *Quercus* and *Eucalyptus* species (except for study 21 on *Fagus sylvatica*). Trees of these genera can develop particularly deep (tap) root systems (Abrams, 1990; Christina et al., 2011) and thinning may provide trees with resources to expand these systems further.

4.3. Thinning benefits for growth following drought decrease over time

In accordance with our second hypothesis, benefits of both moderate and heavy thinning on growth performance following drought (recovery and resilience) decreased with time since the last thinning intervention. This finding is in agreement with recent results for *C. atlantica* stands in southern France, where the highest intensity of thinning improved post-drought recovery of growth for a period of up to ten years but not beyond (Guillemot et al., 2015).

The finding that thinning lag affected growth resistance during drought both negatively and positively in this meta-analysis may be the result of differences in the implementation of the same thinning treatment among studies. For example, the initial difference in stand basal area between thinned and unthinned stands was maintained over time during follow-up interventions in some but not in all studies thus resulting in different trajectories of stand basal area over time within one and the same thinning treatment. For example, only one thinning intervention was conducted over a period of 19 and 43 years in studies 14 and 9, respectively while five interventions took place within 20 and 29 years in studies 5 and 18, respectively (Table 1).

4.4. Resistance and resilience of radial growth to drought decrease with stand age

In accordance with our second hypothesis, we found a negative effect of stand age on the growth response during drought (resistance) as well on the resilience following drought in most stands. Our findings are in line with those of a study on *Pinus resinosa* that reported decreasing thinning benefits for growth resistance and resilience in relation to drought with increasing stand age (D'Amato et al., 2013). This was attributed to the higher water demands of larger, older trees in increasingly open stands (D'Amato et al., 2013). In addition, higher drought sensitivity of large trees was attributed to their greater vulnerability to hydraulic stress and to higher radiation and evaporative demand of the more exposed crowns when compared to smaller trees (Bennett et al., 2015).

However, as opposed to the second hypothesis, recovery following drought was positively (or not at all) but never negatively affected by stand age according to our meta-regression results. In accordance with our explanation for the improved growth recovery following drought in thinned conifer stands, older trees with larger crowns may take faster advantage of improved conditions after drought events. In heavy thinning treatments growth recovery within 3 years after a drought was faster and more complete in older than in younger stands.

However, as discussed before, benefits of thinning for the growth response to drought differed between broadleaves and conifers. Hence the relationship between stand age and the growth response to drought may also differ between these 2 taxonomic groups but due to the small number of studies conducted in broadleaves, we could not conduct separate meta-regressions.

4.5. The relationship between growth response to drought and site aridity differs for moderately thinned stands

In contrast to our fourth hypothesis, we found no uniform positive relationship between the thinning-induced growth response to drought and site aridity. Results of our meta-regression indicated

that growth resistance during drought increased with site aridity in heavily thinned and unthinned stands, whereas site aridity had no or even a negative effect in moderately thinned stands. The opposite was found for the growth performance following drought.

For trees growing in either very open or in closed stands, water limitations during individual drought years seem to have less detrimental consequences for the growth performance during drought but rather led to reductions of recovery and resilience following drought with increasing site aridity. Trees adapted to drier conditions may invest more in non-structural carbon reserves (Maguire and Kobe, 2015) to maintain growth under adverse conditions, but it may be more difficult for them to replenish these reserves and recover growth subsequently.

However, the question still remains why we found such a distinctly different relationship between site aridity and the growth response to drought in moderately thinned stands. Most likely this is attributable to an imbalanced distribution of studies across taxonomic groups, thinning intensities and climatic regions in our meta-analyses. About half of the studies employed only one thinning intensity (in addition to the control), and of these, two thirds compared a heavy thinning to the control. Thus, results referring to moderately thinned stands cover less tree species and a smaller gradient of site aridity than those for unthinned and heavily thinned stands.

4.6. Adaptation potential of thinning and future research needs

This meta-analysis has demonstrated that thinning, in particular heavy thinning is a suitable approach to improve the growth response of trees to drought. Thinning should therefore be considered as an element of active adaptation in forestry. A major finding of this meta-analysis was that the adaptation potential of thinning differs between conifers and broadleaves as in conifers mainly the recovery and resilience of growth following drought is improved whereas in hardwood species, thinning may rather increase the resistance of growth and physiological processes during drought years.

While this meta-analysis has underpinned the value of thinning as an important approach to adapt existing forests to droughts, there are a number of important questions that could not be sufficiently well addressed here. The majority of studies that met selection criteria for a meta-analysis were from temperate and Mediterranean regions while studies from boreal and tropical regions were underrepresented. In addition, the relatively few studies in broadleaved tree species were mainly in Mediterranean oaks.

Another problem that reduced the explanatory power of this meta-analysis was the variability of characteristics of the thinning regime among studies as it is not only characterized by the intensity of a given intervention but also by the frequency, timing and total number of interventions. For example, thinning intensity and frequency had an interactive effect on the growth response of *Pinus sylvestris* to drought (Sohn et al., 2016). However, this could not be tested in this study due to lack of information on the exact timing of follow-up thinning interventions in several studies.

The studies included in this meta-analysis focused exclusively on seasonal or annual drought events. However, the response of trees to thinning may differ for prolonged and recurrent drought events that span several years. Future experiments and analyses of the effect of thinning on the drought response of trees should address the gaps that have been identified in this study.

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Appendix A

Relationships between resistance, recovery, and resilience of radial-growth with site aridity, thinning lag and stand age in differently thinned stands based on meta-regression results. Site aridity was calculated using the HKL-index as suggested by Döring et al. (2011); thinning lag refers to the number of years since the last thinning intervention and stand age at the time of the drought event. For each of the 3 Lloret-indices, we calculated a short-term index using the value referring to 1 year before (for resistance and resilience) or after the drought (recovery and resilience) and (right) a medium-term index using the mean of the 3 years before or after the drought event (see Lloret et al., 2011; Kohler et al., 2010). Values of 1 mean for resistance that no growth reduction has taken place, at 0.5 a 50% reduction occurred. For recovery, a value of 1 means that growth after drought stayed at the level of the drought year. For resilience, a value of 1 indicates that growth after the drought returned to the pre-drought level.

Drought response-indices of radial growth	Thinning treatments	Continuous explanatory variables		
		Site aridity (HKL-) index	Thinning lag	Stand age
Short-term resistance	Unthinned	(+) ^{**}		(-) ^{***}
	Moderately thinned	(-) ^{***}	(+) ^{***}	(-) ^{***}
	Heavily thinned	n.s.	(-) ^{**}	(-) ^{***}
Medium-term resistance	Unthinned	(+) ^{***}		(-) ^{***}
	Moderately thinned	n.s.	(-) ^{***}	n.s.
	Heavily thinned	(+) ^{***}	(+) ^{***}	(-) ^{***}
Short-term recovery	Unthinned	(-) ^{**}		(+) ^{***}
	Moderately thinned	(+) ^{***}	(-) ^{***}	n.s.
	Heavily thinned	(-) ^{***}	(-) ^{***}	(+) ^{***}
Medium-term recovery	Unthinned	(-) ^{***}		(+) ^{**}
	Moderately thinned	(+) ^{***}	(-) ^{***}	(+) ^{***}
	Heavily thinned	(-) ^{***}	(-) ^{***}	(+) ^{***}
Short-term resilience	Unthinned	n.s.		n.s.
	Moderately thinned	(+) ^{***}	(-) ^{***}	(-) ^{***}
	Heavily thinned	(-) ^{***}	(-) ^{***}	(-) ^{***}
Medium-term resilience	Unthinned	n.s.		(-) ^{***}
	Moderately thinned	(+) ^{***}	(-) ^{***}	(-) ^{***}
	Heavily thinned	(-) ^{***}	(-) ^{***}	(+) ^{***}

"n.s." = not significant, "-" = negative slope, "+" = positive slope.

^{**} p < 0.05.

^{***} p < 0.001.

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